Effect of acorn size on development of northern red oak 1-0 seedlings

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Abstract: The effect of acorn size on seedling development was determined for 20 northern red oak (*Quercus rubra* L.) mother tree selections from the USDA Forest Service's Eastern Tennessee Watauga seed orchard. Acorns from each mother tree were visually separated into three size groups, weighed, and sown separately in forest nurseries located in Georgia, North Carolina, and Tennessee. Seedling height, root collar diameter, and survival within sibling seedlots were significantly related to acorn mass. The three sizes of acorns showed the same trends in seedling development among the four nurseries. Heritability (h^2) estimates for the variables were uniformly high among all acorn sizes. A wide range in sibling seedling quality occurred within each acorn size class regardless of nursery location. This suggests that while sizing of acorns into several categories may result in more uniform germination within a seedbed, it will not result in uniform seedling development even when using sibling seedlots and acorns of uniform size.

Résumé : L'influence de la dimension des glands sur le développement des semis a été étudiée chez 20 chênes rouges nordiques (*Quercus rubra* L.). Ces arbres mères ont été sélectionnés dans le verger à graines Watauga du USDA Forest Service situé dans l'est du Tennessee. Les glands de chaque arbre mère ont été séparés à l'œil en trois classes en fonction de leur dimension, puis ils ont été pesés et ensemencés séparément dans des pépinières forestières situées en Georgie, en Caroline du Nord et au Tennessee. La hauteur des semis, le diamètre au collet et le taux de survie dans les lots de graines provenant d'un même arbre étaient significativement reliés à la masse des glands. Les trois classes de dimension des glands montraient les mêmes tendances quant au développement des semis dans les quatre pépinières. Les estimations d'héritabilité (h^2) pour les variables étaient uniformément élevées pour les glands de toutes les dimensions. Il y avait une large gamme de qualités de semis provenant d'un même arbre dans chaque classe de dimension des glands peu importe où la pépinière était située. Ces résultats suggèrent que, même si le classement des glands en fonction de leur dimension peut entraîner une germination plus uniforme dans un lit de germination, cela ne garantit pas un développement uniforme des semis même si on utilise des lots de graines qui proviennent d'un même arbre et des glands de dimension uniforme.

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Introduction

An important problem in the artificial regeneration of oak species is a reliable supply of acorns for seedling production. Some oak species, such as northern red oak (*Quercus rubra* L.), exhibit a high degree of graft incompatibility and therefore are difficult to establish as clonal seed orchards

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(Schlarbaum et al. 1994). The creation of seedling seed orchards of these species is a viable, albeit largely unexplored, alternative to clonal orchards to meet seed demands (Schlarbaum et al. 1993).

In 1973 the Tennessee Valley Authority (TVA) established a northern red oak progeny test at the Watauga Ranger District of the Cherokee National Forest near Elizabethton, Tenn. The test contained 220 open-pollinated families originating from mother trees located throughout the Tennessee Valley. This test site was later converted to a seedling seed orchard in 1987 by the USDA Forest Service to produce acorns for regional reforestation needs and research (LaFarge and Lewis 1987). Initial research in the seed orchard was directed toward evaluation of individual trees for acorn production and other desirable growth and morphological characteristics (Schlarbaum et al. 1994). This research showed that some trees had acorn production as early as age 13. In 1992, it was observed that acorn masses from individual trees in the orchard consistently varied six- to eightfold. Variation in acorn masses within a single mother tree appeared to be as large as the variation among all mother trees in the seed orchard that year. Many of these small acorns (mass <1.5 g) germinated while in cold storage and subsequently produced seedlings when sown in a nursery bed.

However, these smallest acorns appeared to have lower germination energy and capacity than the larger acorns from the same tree.

Little information is available on acorn size and mass distribution from specific mother trees and their affect upon future seedling development. Mass or size of northern red oak acorns from different wild collections may vary up to two-fold, and it is normally assumed that differences have a significant effect on seedling development. However, exceptions to this are so commonly encountered (Korstian 1927; McComb 1934; Jarvis 1963; Olson 1974; Bonner 1987) that a generalized statement about the relationship cannot be made. In order to clarify this relationship, a study was initiated using acorns collected from certain trees in the Watauga seed orchard that produced a wide variety of acorn sizes.

The objectives of this study were to (i) determine ranges in acorn sizes (i.e., masses) within and among 20 northern red oak mother trees, (ii) compare seedling development among mother trees and acorn size classes in different nurseries, and (iii) determine genetic involvement relating acorn sizes to seedling development.

Materials and methods

Acorn collection

Acorns from 20 mother trees located at the USDA Forest Service Watauga seed orchard were collected from late September to mid-November 1993. The open-pollinated half-sib progeny in the seed orchard were from individual mother trees initially located throughout Tennessee, Alabama, Virginia, North Carolina, and Kentucky. However, most trees used here were from Tennessee selections occurring at elevations ranging from 150 to 610 m. (Table 1).

Shade cloth screening was placed on the ground under the canopy in mid-September 1993 to facilitate acorn collection. The acorns were collect daily to prevent excessive drying and predation by deer, turkey, and squirrels. They were tested by water flotation on site immediately after collection. Those acorns that floated were discarded but those that sank were accepted as sound if no insect damage was visible (Olson 1974). The sound acorns were then put in partially sealed plastic bags and placed in cold rooms maintained at 3–5°C until the harvesting was completed in mid-November.

Acorn size classes for each mother tree were determined by mixing and spreading its acorns on a flat surface and visually estimating the largest, medium (average), and smallest size acorns for that mother tree. Then, 240 acorns were chosen at random in each size class for that particular mother tree. The total mass of each 240-acorn lot was obtained, which then was separated into 60-acorn lots. Each 60-acorn lot was again weighed and the average acorn mass was computed (Table 1).

Nursery installation

The acorns were sown in three state forest tree nurseries, the Georgia Forestry Commission's Flint River Nursery, Montezuma, Ga., the North Carolina Division of Forestry's Morganton Nursery, Morganton, N.C., and the Tennessee Division of Forestry's East Tennessee Nursery, Delano, Tenn., and at the USDA Forest Service Institute of Tree/Root Biology's Whitehall Experimental Nursery, Athens, Ga. Initial soil fertility in the four nurseries was adjusted to bring levels of Ca, K, P, and Mg, when practical, to 500, 80, 80, and 50 ppm, respectively, prior to sowing, as recommended by Kormanik et al. (1994). The total N application over the entire growing season ranged from 390 to 560 kg/ha depending on the weather conditions at a particular nursery. The N (as NH_4NO_3) was applied at 2-week intervals during the growing season with the first two applications at 6 kg/ha, the third at 18 kg/ha, the next six at 56 kg/ha, and any additional ones at 37 kg/ha.

The families were randomly assigned to study plots within a nursery bed and a buffer strip of approximately 1.2 m was maintained between plots. The three acorn sizes within each family were then randomly assigned to subplots. Acorns were hand-sown in rows within each subplot at a density of 65/m². Number of rows in each nursery bed differed from four to six in each nursery to standardize row configuration to match nursery equipment.

Seedlings were undercut at a depth of 25–30 cm, lifted, and then evaluated during February and March 1995. Height (HT) and root collar diameter (RCD) were recorded for all seedlings.

Statistical methods

The study consisted of a randomized block, split-plot design where each nursery was a replicate (block). The whole-plot treatment was family (20 levels) and the subplot treatment was acorn size (three levels). For this analysis, both treatment factors were considered fixed, while nursery was a random factor representing replication. The variables analyzed were the mean subplot value of the specific seedling parameters. Analysis of variance was used to evaluate the family and size effects, and Tukey's multiple comparison procedure was used to find specific treatment mean differences. This analysis was applied to data based on the mean obtained from all the seedlings in a subplot pertaining to HT, RCD, and survival.

Within each acorn size class, linear regressions of subplot mean values of HT and RCD were developed as a function of mass. The observations were the mean subplot values for HT, RCD, and mass for all families. It was known that differences exist among the nurseries with respect to basic fertility levels maintained, as well as other edaphic and environmental factors, so these regression equations were developed for each individual nursery. Thus, the separate regressions maintained the benefit of blocking, which reduced variability. Initially, these regressions were developed for each acorn size class, but they were generalized over a wider range of masses by pooling all the acorn size classes and then developing regressions.

The genetic component of this study was addressed in two ways. First, family heritability (h^2) values and standard errors (SE) were computed for each variable separately for each acorn size class. This was accomplished by treating the original split-plot design as three randomized block designs (one for each acorn size class) and assuming that nursery and family were random factors. Second, to determine the relative contribution of nursery, family, and size to total variation, an analysis of the variance components was performed assuming the original split-plot design where all three factors were considered random effects. PROC VARCOMP (SAS Institute Inc. 1988) was used to perform the computations using the MIVQUE0 method.

Results

Edaphic and environmental conditions at each nursery location had significant influence on seedling development from different-sized acorns, but the trends in seedling relative growth rates were comparable by acorn size from all nursery locations.

Effects of family and acorn size

No interactions existed at the 0.05 significant level in the split-plot analysis for family and acorn size; thus, main effects could be easily interpreted (Table 2). Family and acorn

Table 1. Nursery location (1993), tree orchard number, state, county, elevation, and acorn masses by acorn size class (S, small; M, medium; L, large) by family selected from the 1993 acorn crop.

Tree orchard No.	State	County	Elevation (m)	Mean acorn mass (g)														
				1973 average	Flint, 1993			Whitehall, 1993			North Carolina, 1993			Tennessee, 1993		
					S	M	L	S	M	L	S	M	L	S	M	L
1-10-100	Virginia	Wise	450	5.03	1.62	3.59	5.69	1.61	3.69	5.61	1.65	3.71	5.59	1.61	3.61	5.69
1-10-507	Tennessee	Union	425	7.08	1.60	3.60	7.62	1.58	3.61	7.66	1.61	3.53	7.66	1.61	3.60	7.61
1-19-577	Tennessee	Morgan	610	6.89	1.58	3.49	5.92	1.68	3.55	6.10	1.42	3.48	6.06	1.56	3.49	6.06
1-1-580	Tennessee	Claiborne	365	6.28	2.61	5.64	8.95	2.42	5.62	8.96	2.42	5.57	8.75	2.46	5.67	8.91
1-6-557	Tennessee	Morgan	610	6.89	1.79	3.89	6.79	1.83	3.89	6.81	1.87	3.99	6.90	1.78	3.92	6.86
2-10-1164	Tennessee	Monroe	610	4.11	1.40	3.48	6.02	1.45	3.51	6.12	1.43	3.44	6.01	1.47	3.39	6.17
2-10-530	Tennessee	Morgan	610	5.5	2.20	4.04	7.20	2.19	4.04	7.15	2.12	4.00	7.15	2.16	4.08	7.10
2-11-2451	Tennessee	Anderson	305	3.5	1.19	3.20	4.63	1.23	3.20	4.61	1.22	3.11	4.57	1.18	3.13	4.61
4-11-526	Tennessee	Morgan	610	4.99	1.29	3.68	5.67	1.31	3.66	5.67	1.35	3.72	5.55	1.34	3.70	5.58
4-24-613	North Carolina	Transyla	610	4.82	1.79	4.51	6.20	1.74	4.60	6.19	1.73	4.61	6.25	1.68	4.49	6.21
4-2-902	Tennessee	Henderso	150	6.83	1.10	4.34	7.77	1.09	4.32	7.81	1.06	4.29	7.75	1.11	4.32	7.71
4-6-626	Tennessee	Campbell	365	5.57	1.69	3.53	5.24	1.69	3.54	5.54	1.66	3.55	5.32	1.68	3.59	5.41
5-11-701	Tennessee	Anderson	305	5.38	1.64	3.55	5.56	1.61	3.48	5.49	1.61	3.56	5.57	1.56	3.50	5.48
5-12-632	Tennessee	Henderso	150	4.39	1.15	3.33	5.20	1.20	3.37	5.16	1.17	3.36	5.13	1.18	3.36	5.13
5-2-582	Tennessee	Claiborne	365	6.13	1.85	4.62	6.90	1.86	4.61	6.88	1.77	4.61	6.88	1.83	4.60	6.97
6-2-913	Tennessee	Henderso	150	7.84	1.69	4.16	7.24	1.67	4.05	7.40	1.61	4.09	7.36	1.62	4.17	7.26
6-6-2419	North Carolina	Buncombe	910	5.61	1.48	5.13	9.05	1.42	5.19	9.02	1.44	5.15	9.09	1.43	5.10	9.01
6-7-550	Tennessee	Campbell	335	6.06	2.35	4.28	5.63	2.34	4.26	6.52	2.35	4.23	6.26	2.35	4.25	6.34
7-15-605	North Carolina	Buncombe	1060	5.43	1.75	3.81	6.19	1.75	3.83	6.15	1.75	3.79	6.16	1.72	3.81	6.11
8-8-330	Kentucky	Trigg	150	4.99	1.67	5.03	7.47	1.64	5.11	7.46	1.62	5.02	7.41	1.66	5.04	7.45

Table 2. Analysis of variance results (P values) for 20 northern red oak families and three acorn sizes.

Source	df	HT	RCD	Survival percentage
Site	3	—	—	—
Family	19	0.0007	0.0006	0.0001
Error (a)	57	—	—	—
Size	2	0.0001	0.0001	0.0001
Family × size	38	0.1843	0.3155	0.3738
Error (b)	120	—	—	—
Total	239			

Note: HT, height (cm); RCD, root collar diameter (mm).

Table 3. Least square means of progeny from 20 northern red oak families.

Family	HT (cm)	RCD (mm)	Survival percentage
1-1-580	75.9a	9.72a	72.8ef
1-10-100	60.2ab	8.0b	83.6abcde
1-10-507	66.6ab	8.4ab	81.2abcdef
1-19-577	55.1b	8.1b	81.8abcdef
1-6-557	62.3ab	8.9ab	87.2abcd
2-10-1164	62.0ab	8.6ab	75.4bcdef
2-10-530	65.5ab	8.2b	88.1abc
2-11-2451	53.2b	7.9b	81.4abcdef
4-11-526	59.1ab	8.12b	90.6a
4-2-902	59.4ab	7.7b	72.9ef
4-24-613	57.1b	8.5ab	86.4abcde
4-6-626	55.2b	7.7b	90.8a
5-11-701	52.8b	8.4ab	78.1abcdef
5-12-632	55.0b	8.1b	69.7f
5-2-582	62.8ab	8.7ab	74.9cdef
6-2-913	60.2ab	8.1b	86.2abcde
6-6-2419	58.3b	8.4ab	78.8abcdef
6-7-550	64.1ab	8.2b	89.2ab
7-15-605	55.8b	8.2b	73.9def
8-8-330	68.4ab	8.8ab	83.3abcdef

Note: Means followed by the same letter for a given variable are not significantly different at the 0.05 level based on Tukey's test. HT, height; RCD, root collar diameter.

Table 4. Least square means of height (HT), root collar diameter (RCD), and survival percentage for three acorn sizes from 20 northern red oak families.

Size	HT (cm)	RCD (mm)	Survival percentage
Small	47.8a	7.25a	70.4a
Medium	63.0b	8.56b	85.6b
Large	70.6c	9.29c	88.0b

Note: Means followed by the same letter for a given variable are not significantly different at the 0.05 level based on Tukey's test.

size significantly affected HT, RCD, and survival. The individual family and acorn size least square means for each variable are given in Tables 3 and 4, respectively, along with all pairwise multiple comparison tests. Since the seed orchard was established from selected trees that were all of above-average quality in a tree improvement program, the progeny exhibited uniform growth that resulted in no clear-cut differences among the families. Thus, superiority was difficult to distinguish, although several groups could be deduced. Significant differences were clearly observed for HT and RCD among all three size classes, with the small acorns exhibiting lower values than the medium acorns, which had lower values than the large acorns. Survival percentage exhibited the same trend, although differences between medium and large acorns were not significant.

Further insight into the effects of family and size may be obtained by investigating acorn size within family. Although the previous analysis indicated a significant size effect, it is of interest to note that the distributions of seedling responses (HGT and RCD) for the three sizes within a family possess significant overlap due to a high degree of variability. Table 5 shows statistics on the minimum, maximum, and mean for each size class within each family. It was readily apparent that poor and good seedling characteristics are obtained from all three size classes. This was more clearly illustrated by frequency distributions, such as those shown in Fig. 1, for two individual families. When combined over family, similar distributional overlap is seen for each of the four nurseries (Fig. 2). Hence, although relative acorn size within a family is a significant factor, good seedlings may be obtained from all size classes. In addition, when combining acorn sizes among families, it is important to also consider absolute acorn size.

Relationship of acorn mass to seedling size

Regressions of HT and RCD on mass for the large acorn size showed that all nurseries except Whitehall had significant slope coefficients for HT, while all except North Carolina were significant for RCD. The regressions were also performed for the small and medium acorn size classes and they exhibited similar patterns of significance levels for HT and RCD (data not shown). The regressions for the pooled data (all three size classes) are given in Fig. 3. In all cases, the slope coefficients were significant and the R^2 values were greater than 0.40. The slope of the line indicates the rate of increase in HT or RCD with a 1-g increase in acorn mass. At the North Carolina, Flint, and Tennessee nurseries, HT and RCD increased by about 4 cm and 0.32 mm, respectively, per gram increase in acorn mass whereas at the Whitehall nursery, HT and RCD increased at approximately twice this rate per gram increase in acorn mass.

Genetic aspects

Estimates of h^2 were quite large for HT, RCD, and survival with acceptably small SEs (Table 6). No trends in heritability were observed over acorn size classes. An analysis of the variance components due to nursery, family, and size indicated the relative contribution of each of these factors to total variation (Table 7). The nursery effect accounted for the largest variation, ranging from 27.7 to 46.2% of total variation for all three variables. Acorn size was also very important, being comparable in importance for HT and survival but somewhat less for RCD. The family variance component was small and amounted to approximately 10% or less.

Table 5. Descriptive statistics based on the individual seedling data pooled over all four nurseries for each family and acorn size (S, small; M, medium; L, large).

Family	Size class	All seedlings HT (cm) Min.	Max.	Mean	RCD (mm) Min.	Max.	Mean
4-2-902	S	10	103	34.6	2.4	10.6	5.3
	M	17	169	65.8	3.6	14.7	8.1
	L	12	184	78.0	2.3	17.2	9.4
1-10-100	S	8	130	46.3	2.0	14.9	6.8
	M	8.4	138	60.8	3.0	15.0	8.1
	L	11	176	73.0	3.4	15.8	8.9
1-10-507	S	11	160	50.6	2.4	15.6	6.8
	M	12	180	65.8	2.8	17.8	8.5
	L	11	192	81.4	2.8	16.2	9.7
4-11-526	S	5.0	125	47.6	2.3	13.7	7.1
	M	12.0	160	64.0	2.8	15.5	8.6
	L	7.0	157	64.2	3.1	16.8	8.5
2-11-2451	S	11.0	123	38.2	2.1	13.6	6.4
	M	8.0	147	54.8	1.7	14.8	8.5
	L	9.0	156	65.7	2.4	15.4	8.7
6-2-913	S	11.0	105	43.9	2.4	14.6	6.9
	M	12.0	151	61.9	2.8	14.6	8.2
	L	9.6	155	75.3	2.5	16.4	9.4
1-19-577	S	9.0	134	41.6	2.4	13.4	6.8
	M	10.0	157	57.2	2.5	15.7	8.2
	L	7.0	165	67.2	2.8	15.7	9.5
2-10-530	S	6.0	117	51.8	1.0	13.4	7.3
	M	12.0	156	69.6	3.5	15.9	8.4
	L	16.0	155	76.5	3.4	16.8	9.2
6-7-550	S	9.0	141	55.7	2.8	15.1	7.5
	M	8.0	145	62.1	2.5	15.0	8.1
	L	14.0	165	74.3	0.7	17.2	9.0
5-11-701	S	8.0	108	44.2	2.4	15.0	7.8
	M	11.0	155	52.7	2.0	18.0	7.9
	L	8.0	160	60.8	2.7	17.2	9.4

Family	Size class	All seedlings HT (cm) Min.	Max.	Mean	RCD (mm) Min.	Max.	Mean
1-6-557	S	7.0	143	51.0	1.6	13.9	7.6
	M	13.0	141	67.2	1.7	15.4	9.6
	L	13.0	131	67.6	3.3	19.6	9.7
4-24-613	S	6.0	119	49.1	2.2	16.9	8.0
	M	11.0	125	60.7	2.3	15.4	8.7
	L	9.0	163	61.3	2.5	15.5	8.8
4-6-626	S	8.0	144	44.6	2.3	14.8	6.8
	M	5.0	150	58.8	2.0	16.7	8.1
	L	7.0	165	60.4	2.1	16.7	8.3
5-12-632	S	9.0	95	41.3	2.1	11.7	6.9
	M	9.0	139	60.4	2.0	16.6	8.2
	L	9.0	143	61.2	3.0	17.1	8.8
6-6-2419	S	4.0	126	42.6	2.8	15.8	6.8
	M	9.0	133	61.2	2.5	19.3	8.8
	L	6.0	165	67.6	2.0	18.0	9.2
2-10-1164	S	9.0	159	49.4	2.7	15.3	7.5
	M	10.0	145	65.3	2.1	16.6	8.7
	L	13.0	159	76.4	2.8	19.9	9.8
8-8-330	S	10.0	137	52.9	2.1	13.4	7.5
	M	12.0	191	70.2	3.3	18.1	8.9
	L	16.0	190	81.9	3.2	20.6	10.1
5-2-582	S	7.0	155	49.8	1.4	14.5	7.4
	M	9.0	168	66.0	2.7	17.6	9.2
	L	10.0	167	74.9	3.2	17.4	9.6
1-1-580	S	13.0	191	70.3	2.6	15.5	8.6
	M	12	163	75.0	3.0	15.7	9.9
	L	23	209	85.9	3.9	17.7	10.7
7-15-605	S	10.0	120	43.3	2.3	17.0	7.0
	M	7.0	142	60.7	2.3	18.2	8.6
	L	11	152	62.3	2.6	20.0	9.0

Note: HT, height; RCD, root collar diameter.

Table 6. Heritability (h^2) estimates and standard errors (SE) for the three acorn size classes.

	All seedlings		
	HT	RCD	Survival percentage
Small			
h^2	0.699	0.707	0.741
SE (h^2)	0.140	0.136	0.120
Medium			
h^2	0.596	0.478	0.578
SE (h^2)	0.188	0.243	0.196
Large			
h^2	0.642	0.600	0.766
SE (h^2)	0.166	0.186	0.109

Note: HT, height (cm); RCD, root collar diameter (mm). Heritabilities and SEs are given by

$$h^2 = \frac{MS_F - MS_{R \times F}}{MS_F}$$

$$SE(h^2) = \left[\frac{2d^2(d + n - 2)}{n(d - 2)^2(d - 4)} \cdot \frac{MS_{RF}^2}{MS_F^2} \right]^{0.5}$$

where d is df for family, MS_F is mean square for family, MS_{RF} is mean square for the replication × family interaction, and n is df for replication × family interaction.

Table 7. Estimates of the variance components (and percentages of total variance in parentheses) under the split-plot model assuming that nursery, family, and size are random factors.

Variance component	HT	RCD	Survival percentage
Nursery	143.5 (37.8)	1.61 (46.2)	90.2 (27.7)
Family	21.0 (5.5)	0.14 (3.9)	34.7 (10.7)
Nursery × family	26.9 (7.1)	0.08 (2.4)	0.0* (0.0)
Size	134.3 (35.4)	1.06 (30.6)	89.4 (27.4)
Family × size	3.1 (0.8)	0.02 (0.5)	2.1 (0.6)
Error	50.6 (13.3)	0.57 (16.4)	109.4 (33.6)
Total	379.6	3.47	325.8

Note: HT, height (cm); RCD, root collar diameter (mm).

*The computed value of this variance component was −8.9, but because negative values are impossible, it was set equal to 0.0.

Discussion

Edaphic, environmental, and to some extent management philosophies at each nursery had significant influence on seedling development, which is reflected by the regressions in Fig. 3. However, these nursery effects did not alter the significant influence of acorn size on seedling development. Survival percentage (Table 3) for the three acorn sizes must be interpreted with caution because of multiple embryos that characteristically resulted in smaller seedlings with inferior root development regardless of acorn size. Families 4-11-526 and 4-6-626 had seedlings arising from multiple embryos at all four nurseries, and families 1-19-577, 1-1-580, 4-24-613, and 5-11-701 had multiple embryos in at least one nursery. The importance of this trait cannot be ascertained from these data because the seedlings were lifted in three nurseries and

Fig. 1. Distribution of seedling height for each acorn size class for families 1-1-580 and 1-19-577 at the Flint nursery.
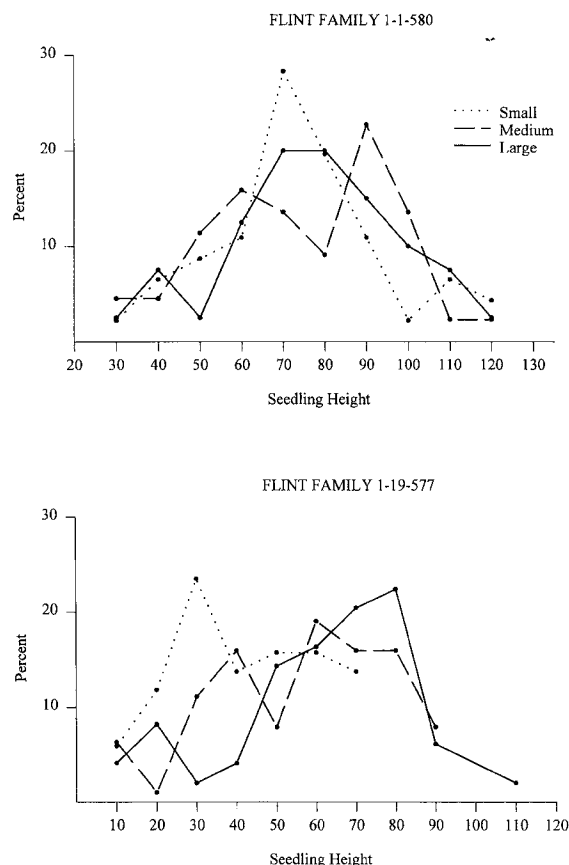
packaged for final evaluation before the extent of the multiple embryos was appreciated.

Among acorn size classes, differences in germination percentage and differences in energy both affected early seedling development. The epicotyls of the small acorns began elongating several weeks later than the epicotyls of the other two acorn sizes in all families and nurseries, and those seedlings were consistently smaller throughout the growing season and had, in general, poorly developed root systems. Seedlings with inferior root development are not competitive in the nursery or when used for artificial regeneration. (Schultz and Thompson 1992; Kormanik et al. 1998a).

Korstian (1927), McComb (1934), and Jarvis (1963) have clearly shown the competitive advantages that acorn size confers on developing seedlings even when ranges in acorn size do not vary as much as they did in this study. McComb (1934) showed that small chestnut oak (*Quercus prinus* L.) acorns had poorly developed root systems with significantly smaller numbers of lateral roots. His results support our present study with northern red oak. He also reported that as size differential became larger between specific acorn size classes, the difference among root systems became more pronounced. We observed this with northern red oak in our study. As with chestnut oak, the northern red oak with larger acorns developed larger root systems (McComb 1934). However, a wide range of seedling sizes was obtained within a family regardless of acorn size. This fact essentially nullified our long-term goal of developing a nursery protocol of

Fig. 2. Distribution of seedling height for each acorn size class for all families combined at each nursery.

FLINT

TN

NC

WHITEHALL
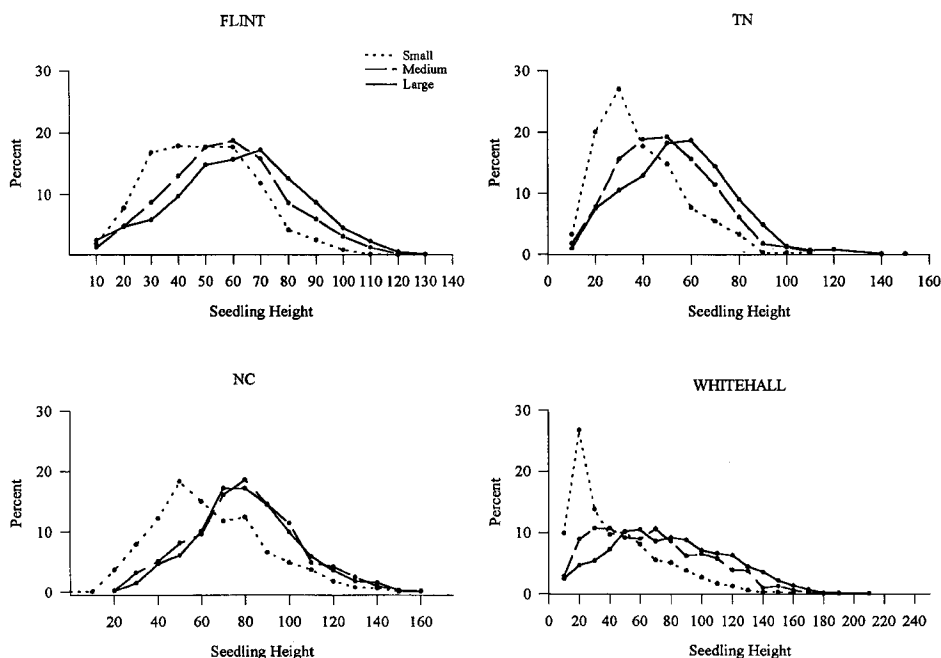
sowing graded acorns instead of grading northern red oak seedlings after they are lifted from the nursery.

Jarvis' (1963) acorn sizing research contained detailed physiological as well as morphological observations. He reported that the physiological advantage of large acorns is based on depletion of carbohydrate reserves in the cotyledons. He found that while relative seedling growth rates were similar regardless of acorn size, the cotyledon carbohydrate reserves were mobilized when environmental conditions limited photosynthesis. It was suggested that the primary advantage for the larger acorns lies not only in being larger "but in being larger at the right time." However, although carbohydrate reserves of large acorns are important, large acorns will not produce uniformly large seedlings even within sibling seedlots.

Separation of acorns by size class from specific mother trees may not be practical for wild collections but will be essential as oak seed orchards come on line.[2] In the seed orchard, we found that acorn size was related to acorn position and branch order and was unrelated to pollen incompatibility problems for the following reasons. The crowns have been released for many years and all trees have adequate growing space. Adequate supplies of unrelated pollen sources are assured because of the initial planting design and subsequent thinnings. The lateral branches have frequently elongated at least 1 m and second- or third-order lateral branch growth provides a full and dense crown.

Along the first-order branches, acorn size decreases basipetally, i.e, those acorns closest to the foliage, and thus, food production yields the largest acorns. The smallest acorns develop primarily on the second- and third-order lateral branches whose leaves are characteristically shaded and

Fig. 3. Regression equations for predicting seedling height (HT) from acorn mass (M) for all acorn mass classes at each nursery.

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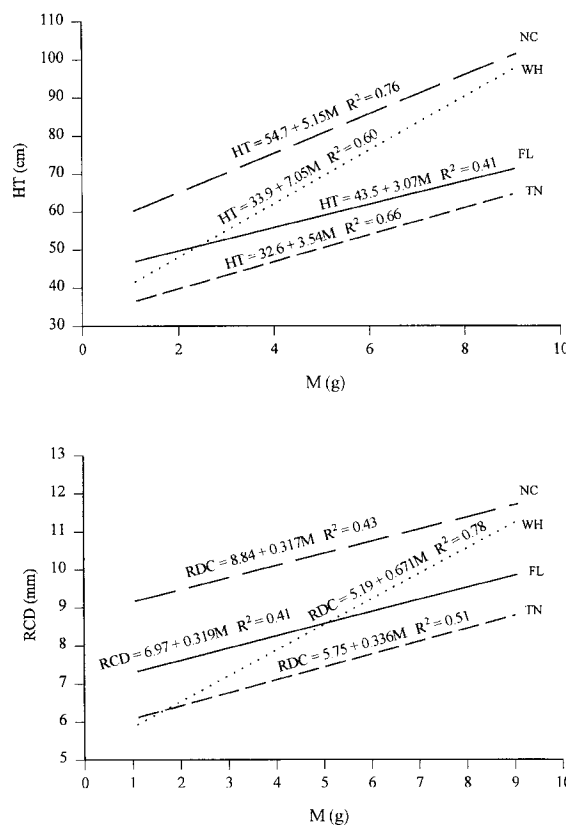
[2] Data on file, Dr. Scott Schlarbaum, Department of Forestry, Wildlife and Fisheries, University of Tennessee, Knoxville, TN 37901-1071, U.S.A.

have reduced photosynthesis capacity (Sung et al. 1998). Thus, it appears that photosynthesis and positional effects are the primary causal factors affecting acorn size within individual selections rather than lack of adequate pollination and fertilization.

Based on results obtained here, when collecting from seed orchards, the smallest northern red oak acorns (i.e., those ≤3 g) might reasonably be discarded and the remainder divided into two or three distinct sizes and sown in the nursery in separate beds. This procedure, however, will not eliminate the high proportion of individuals of undesirable size with inferior root morphology regardless of initial acorn size (Schultz and Thompson 1992). These poorly developing seedlings may represent 30–40% of the population from any specific mother tree regardless of average acorn size (Kormanik et al. 1998b). In the present study, we found no relationship between acorn size and elevational ranges of the initial field selection. Furthermore, no information is available on how initial acorn masses or elevational occurrence affected initial progeny test evaluation in 1973. It is quite possible that a real difference in elevation response may have been effectively masked in this current test because of availability of pollen from 170 families which were from a range of elevational zones and still maintained in the seed orchard.

Height and diameter heritability estimates based on acorn sizes were comparable with those reported by others for different tree species where seed size was not a variable (Jourdain and Olson 1983; Stauder and Lowe 1983; Kormanik et al. 1998b). However, family effects, although significant, were almost inconsequential compared with nursery and acorn size. The distribution of variance as indicated in this study implies that it is more important to perhaps emphasize selection of the largest acorns and use the best nursery protocols for seedling production than to be overly concerned about family superiority. This is especially evident when regressions among nurseries are considered. Early rapid development of many large seedings at the Whitehall nursery severely impacted growth of the smaller seedlings from comparable size acorns. Once overtopped early in the season, these seedlings were never able to obtain a competitive crown position.

Conclusions

Individual mother trees in the Watauga northern red oak seed orchard produce acorns that characteristically vary in mass by six- to eightfold. In all families and all four nurseries, the smallest acorns had the poorest germination and seedling survival. Separation and sowing acorns by uniform size classes did not result in uniformity in seedling growth. Thus, a third or more of the seedlings produced few, if any, lateral roots regardless of acorn mass. Seedling size is related to first-order lateral root (FOLR) numbers, but even the smallest acorn sizes produced some acceptable, although smaller, seedlings at all nurseries. Multiple embryos frequently occurred and usually produced the smallest seedlings with extremely inferior stem growth and root development. This research clearly demonstrates that the larger the acorn the larger the seedling but that larger acorns of themselves do not necessarily yield large seedlings.

Acknowledgements

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